A Short History of Fig Wasp Research

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For convenience, the history of fig wasp research may be divided into four periods. Mayer's "Zur Naturgeschichte der Feigeninsecten" (1882) appears to present the first natural break. On the one hand, in giving a comprehensive review of older literature, it is the conclusion of its period. On the other hand, in being one of a number of contemporaneous reports on exotic fig wasps and, above all things, as a precursor to Mayr's paper of 1885, it also is the opening of a new era. In a way, Grandi's revision of the Agaonidae described by Mayr, and its accessory world catalogue (1928d), would form a similar stage half a century later. Between the two, past the times that scientists merely looked all wonder at figs and their wasps, we find the period in which the warp of fig wasp taxonomy was stretched. Some of the weft, it is true, was of very inequal capacity.

After 1928 we find more than a quarter-century of miscellaneous reports, waifs and strays in comparison with Grandi's synthesis. Then, in the fifties, a new activity arises with a gradual shift of interest to the symbiosis of figs and wasps, its mechanism and evolution.

In the present review I shall not confine myself to data on the Agaonidae. In the survey of our knowledge of fig wasp biology, we cannot dispense with their Torymid mess-mates. An outline of their nomenclatorial history is included in the first chapters. For data on pre-Linnean literature, and for a more complete discussion of eighteenth-century papers, I here refer to Mayer's review of 1882: their biological significance is negligible.

Wonder (the period before Mayer, 1882)

In the "Systema Naturae", Linnaeus named two fig insects viz., *Cynips psenes* from oriental *Ficus carica* and *C. sycomori* from the sycomore fig of Egypt. These insects were generally misidentified until a hundred years later largely, it would seem, because of the confusion created by Linnaeus himself.

Linnaeus' pupil Hasselquist (1757), in his itinerary of a voyage to Palestine, described *Cynips ficus* and *C. caricae* from *Ficus carica,* and *C. cycomori* from *F. sycomorus* (see table 1 for a concise survey of the nomenclatorial history). These descriptions, with only a few small alterations, were repeated in the second part added to the German translation of the "Iter" (1762). In the meantime Linnaeus, presumably having decided that *Cynips ficus* and *C. caricae* probably were the two sexes of one species, united them under the name *Cynips psenes.* The original description of *C. ficus* "corpus totum rufum" and thus, implicitly, the description of *C. psenes,* did not seem to fit the shiny black insect Gravenhorst (1829) described as *Blastophaga grossorum:* the nomenclatorial outcome of a pronounced sexual dimorphism.

Linnaeus (1758) redescribed *Cynips sycomori* and unfortunately added a character of the Agaonidae "antennae ... basi crasso-conicae". This, and the inadequate labels of the specimens in the Linnean Cabinet (Saunders in Waterhouse, 1881), led Westwood (1840) to the description of *Blastophaga sycomori,* which soon proved to be identical with *C. psenes* (see Loew, 1843). Genuine *C. sycomori* was renamed *Sycophaga crassipes* Westwood (1840) although Forskal, as early as 1775, knew both sexes of what he rightly named *Cynips sycomori.*

There remain *Cynips caricae,* and *Ichneumon ficarius* Cavolini, 1782. Loew (1843), "auf Linné's Autorität", accepted the identity of *Cynips ficus* and *C. caricae,* but according to Waterhouse (1881) the two must certainly be considered distinct species. Confusion was complete when Saunders (1883a: 20) listed three species of *Blastophaga* viz.,

sp.1. *B. ficus,* Hasselq.; *C. psenes,* Linn.; *B. sycomori,* Westw.

sp.2. *B. caricae,* Hasselq.; *C. psenes,* Linn.

sp.3. *B. grossorum,* Grav.

Half a year later, Saunders (1883c) alluded *Cynips caricae* to *Idarnella* Westwood (*Idarnodes* Westwood, both names of 1883: a, and c, respectively) for which, however, *Philotrypesis* Förster (1878) proved to be an older name. Except for Mayer, 1882 (and later, myself: Wiebes in China, 1962) no one seems to have recommended the use of the specific epithet *ficarius* as used by Cavolini, 1782. In a way, Westwood (1883c: vii) did, but he regarded *ficarius* distinct from *caricae.*

Table 1. Survey of the nomenclatorial history of *Blastophaga psenes, Philotrypesis caricae* and *Sycophaga sycomori.*

	Blastophaga psenes (Linnaeus, 1758)		*Philotrypesis caricae* (Linn. in Hass., 1762)	*Sycophaga sycomori* (Linnaeus, 1758)
Linn. in Hass., 1757		*Cynips ficus*	*Cynips caricae*	*Cynips cycomori*
Linnaeus, 1758		← *Cynips psenes* →		*Cynips sycomori*
Linn. in Hass., 1762		*Cynips ficus*	*Cynips caricae*	*Cynips sycomori*
Forskal, 1775				*Cynips sycomori*
Cavolini, 1782		*Ichneumon psenes*	*Ichneumon ficarius*	
Gallesio, 1820		*Chalcis psenes*	*Chalcis centrinus*	
Gravenhorst, 1829	*Blast.grossorum*			
Westwood, 1840		*Blast.sycomori*		*Sycophaga crassipes*
Loew, 1843	← *Blast.psenes* →			*Sycophaga sycomori*
Förster, 1878			*Philotrypesis longicauda*	
Saunders, 1878	*Blast.grossorum*	*Blast.psenes*		*Sycophaga crassipes*
Waterhouse, 1881	*Blast.grossorum*	*Blast.ficus*	[*Cynips caricae*]	*Sycophaga sycomori*
Westwood, 1882	← *Blast.psenes* →			*Sycophaga crassipes*
Mayer, 1882	*Blast.grossorum*		*Ichneumon ficarius*	*Sycophaga sycomori*
Saunders, 1883a	*Blast.grossorum*	*Blast.ficus*	*Blast.caricae*	*Sycophaga crassipes*
Saunders, 1883c			*Idarnella caricae*	
Westwood, 1883c			*Idarnodes caricae* *Idarnodes ficarius*	
Mayr, 1885	← *Blast.grossorum* →		*Philotrypesis caricae*	*Sycophaga sycomori*

It took two recent decisions (1964, Opinion 694; 1974, Opinion 1018) to validate *Philotrypesis caricae* (Linnaeus in Hasselquist, 1762) as the name of the common inquiline of *Ficus carica,* in the same sense as it had been used by Mayr (1885), Grandi (1921b, 1930) and Joseph (1958). In the opinion of 1964, *Blastophaga psenes* (Linnaeus, 1758) was validated as the name for the pollinating insect.

Dalman (1818) expressed his wonder in the name of the fig insect he described from Sierra Leone: *Agaon paradoxum. Agaon* was taken as the basis of the family name by Walker (1846), after Westwood recognized the affinities of *Agaon* and *Blastophaga* and, like Latreille (1825), classified them with the Chalcididae. Billberg (1820) as well as later Schulz (1906) emended *Agaon* to *Agaum;* Kieffer (1911) would create a synonym *Courtella* (see Wiebes, 1968b).

It is unfortunate that the specimens recorded by Coquerel (1855) from La Réunion cannot now be found, and are probably lost. Three out of four of his species from *Ficus terragena* (probably, the same as *F. mauritiana* Lam.) are types of generic names viz., *Sycocrypta* with *S. coeca,* suppressed in Opinion 682 (1963) for *Ceratosolen* Mayr, 1885; *Apocrypta* with its type *A. perplexa,* and with *A. paradoxum* which belongs to *Sycophaga* Westwood, 1840; and *Chalcis explorator,* which was taken by Ashmead (1904a) as the type of *Apocryptophagus*: most probably it is one of the Sycoryctini, and not *Idarnes* as Walker (1871b: 60) suggested, nor *Sycophaga* as Westwood (1883b: 379) had it.

Motschulsky's (1863) material I have seen in the Moscow Natural History Museum. *Platyscapa frontalis* belongs to *Waterstoniella* Grandi, 1921a; *Platyneura testacea* most probably is a species of *Parakoebelea* Joseph, 1957a. Validation of the older names would create nomenclatorial changes in the Agaonidae and Torymidae.

From the West Indies Walker (1843) described *Idarnes carme,* which seems to be the same as *Tetragonaspis* Mayr, 1885 (as Mayr supposed but could not decide from Walker's description). This leaves the Old World species of "*Idarnes*" without a generic name (see Wiebes, 1966a: 155–156; 1968a: 310–311), but see the suggestion by Gordh (1975: 439) that *Idarnomorpha* Girault (1915b) could serve. Compare, however, also Hill (1967d: 94), who listed *Idarnomorpha* as a synonym of *Otitesella* Westwood! The type of *I. carme* is a female specimen in the British Museum (Natural History), from which the head was already lost when Westwood (1883a: 37, note) studied it; now it seems to be completely lost, and a neotype had to be designated (Gordh, 1975: 426–427). In the same 1843 paper Walker described *Paphagus* (Walker, 1871b: 65, "*Paphagus Sidero* ... belongs to the Agaonidae"), which was also by Mayr (1885: 151) mentioned as if he supposed it to be a fig wasp. Ashmead (1904a: 319, 499) cited it as one of the Pteromalidae. More confusion was created by Walker's description of wasps destructive to the fig in India, originally in 1871 (b), and again (posthumously) with different names in 1875 (see Patton, 1884; Wiebes, 1967e: 400–402).

In all, by the time Mayer wrote his review, there were known eighteen fig wasps, be they under twenty-four names. Most of these were known in one sex only, but they represented a fair sample of all but one of the larger groups now recognized (see table 2). Their host figs, as far as then known, belong to *Urostigma* (*Ficus benghalensis* from India), *Ficus* (*F. carica*), and *Sycomorus* (*F. sycomorus* from Egypt, and *F. mauritiana* from La Réunion).

Although Linnaeus (Hegardt, 1749) already explained the process of caprification by supposing that the insects brought the farina from the wild fig, which contained male flowers, to the domestic fig, which contained only female flowers (see Westwood, 1840: 215), several authors doubted or opposed this explanation. Mayer (1882, partly basing himself on Solms, 1882) extensively dwelled on this point. Most of his views on *Ficus carica* were corroborated by data from Grandi (1920a, 1929a), Buscalioni & Grandi (1936, 1938), and Joseph (1958), and will be discussed in a later chapter.

Table 2. Fig wasps known in 1882.

AGAONIDAE	proper name	reference
-see table 1-	*Blastophaga psenes* (L., 1758)	Joseph, 1958: 201
Agaon paradoxum Dalman, 1818	*Agaon paradoxum* Dalman	Wiebes, 1968b: 346
Sycocrypta coeca Coquerel, 1855	*Ceratosolen coecus* (Coquerel)	Opinion 682, 1963
Platyscapa frontalis Motschulsky, 1863	*Waterstoniella frontalis* (Motsch.)	(new comb.)
TORYMIDAE, Sycophaginae		
-see table 1-	*Sycophaga sycomori* (L., 1758)	Wiebes, 1968a: 311
Idarnes carme Walker, 1843	*Idarnes carme* Walker	Gordh, 1975: 425
Apocrypta paradoxa Coq., 1855	*Sycophaga paradoxa* (Coquerel)	Westwood, 1883b: 379
Platyneura testacea Motschulsky, 1863	*Parakoebelea testacea* (Motsch.)	(new comb.)
Apocrypta perplexa Coquerel, 1855	*Apocrypta perplexa* Coquerel	Westwood, 1883b: 379
Chalcis explorator Coquerel, 1855	*Apocryptophagus explorator* (Coq.)	Ashmead, 1904a: 238
Idarnes stabilis Walker, 1871	*Sycoscapter stabilis* (Walker)	Wiebes, 1967e: 407
Idarnes orientalis Walker, 1875		
-see table 1-	*Philotrypesis caricae* (L. in Hass.)	Joseph, 1958: 201
Idarnes transiens Walker, 1871	*Philotrypesis transiens* (Walker)	Opinion 1018, 1974
Polanisa lutea Walker, 1875		
Sycobia bethyloides Walker, 1871, ☿	*Walkerella temeraria* Westwood	Wiebes, 1967e: 402
Idarnes pteromaloides Walker, 1871	*Micranisa pteromaloides* (Walker)	Wiebes, 1967e: 404
Micranisa Walker, 1875		
TORYMIDAE, Epichrysomallinae		
Sycobia bethyloides Walker, 1871	*Sycobia bethyloides* Walker	Joseph, 1957a: 128
Agrianisa myrmecoides Walker, 1875		
EURYTOMIDAE, Eudecatominae		
Sycophila megastigmoides Walker, 1871	*Sycophila megastigmoides* Walker	Burks, 1969: 119
Pseudisa smicroides Walker, 1875		
Sycophila decatomoides Walker, 1871	*Sycophila decatomoides* Walker	Burks, 1969: 119
Isanisa decatomoides Walker, 1875		

Warp and Woof (from Mayer, 1882 to Grandi, 1928d)

Before 1882 only a few shipments of tropical or subtropical fig insects were sent to Europe. Then, in 1882, Mayer reported on the collections made by Solms, that is, taken from figs in European herbaria or collected in Java, or brought from Egypt by Schweinfurth and Valentiner; moreover, Fritz von Müller (1886–1887) sent several samples from Brazil. Thus began the stream of shipments to Europe, and to America, where research was soon to start.

I shall now discuss some works of more general importance viz., those by Mayr (1885), Ashmead (1904a) and Grandi (1916–1917). Table 3 contains the classification of most of the genera discussed below; a more complete list of the Sycophaginae was presented by Hill (1967d: 92–96).

Mayr distinguished between three categories of fig insects viz., gall makers (according to Mayr: probably all "Agaoninen", certainly those of the genus *Blastophaga*), Hymenoptera parasitic upon larvae and pupae of the gall makers, and visitors ("Feigenbesucher") such as ants and fruit flies. Next to several genera of the modern family Agaonidae, the first group also contained *Crossogaster* and *Sycophaga* (inclusive of *Apocrypta*!). It is now known (Galil, Dulberger & Rosen, 1970) that at least *Sycophaga sycomori* does cause "gall-tissue" in *Ficus sycomorus*. It was mainly the female morphology (the facial groove and other characters related to the way of entering the fig receptable) that characterized the Agaoninae in Mayr's restricted sense (with Walker, the Agaonidae contained all fig wasps). Undoubtedly, Mayr classified his Agaoninae with the Chalcididae. In 1906, Mayr added new records and descriptions.

Table 3. Fig wasp classifications by Saunders, Mayr, Ashmead and Grandi compared.

Saunders, 1883a	Mayr, 1885	Ashmead, 1904a	Grandi, 1928d	recent names
SYCOPHAGIDES				
Prionostomata 1)	"Agaoninen"	AGAONIDAE	AGAONINAE	
		Agaoninae	Agaonini	AGAONIDAE
				Agaoninae
Agaon	*Agaon*	*Agaon*	*Agaon*	*Agaon*
			Alfonsiella	*Alfonsiella*
			Allotriozoon	*Allotriozoon*
			Elisabethiella	*Elisabethiella*
Pleistodontes	*Pleistodontes*	*Pleistodontes*	*Pleistodontes*	*Pleistodontes*
	Tetrapus	*Tetrapus*	*Tetrapus*	*Tetrapus*
				Blastophaginae
Eupristina	*Eupristina*	*Eupristina*	*Eupristina*	*Eupristina*
Sycocrypta				*Ceratosolen*
	Ceratosolen	*Ceratosolen*	*Ceratosolen*.	
Kradibia	*Blastophaga*	*Blastophaga*	*Blast.* s.str.	*Blastophaga* s.l.
Blastophaga				
		Eisenia	*Secundeisenia*	
			Pegoscapus	*Pegoscapus* 2)
			Julianella	
			Valentinella	
			Liporrhopalum	*Liporrhopalum*
		Sycophaginae		
Platyscapa		*Platyscapa*		
			Waterstoniella	*Waterstoniella*
				TORYMIDAE
				Sycophaginae
Haplostomata 1)			Sycophagini 3)	
	Crossogaster	*Crossogaster*	*Crossogaster*	*Crossogaster*
Sycophaga				
Apocrypta	*Sycophaga*	*Sycophaga*	*Sycophaga*	*Sycophaga*
paradoxa				
perplexa		*Apocrypta*	*Apocrypta*	
	-.-.-	TORYMIDAE	TORYMIDAE	*Apocrypta*
		Idarninae	Idarnini	
	Goniogaster	*Goniogaster*	*Goniogaster*	
SYCOLACIDES				
Idarnes etc.	*Idarnes* etc.	*Idarnes* etc.	*Idarnes* etc.	*Idarnes* etc.

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[1] These names are emendations of Prionastomata and Aploastomata, respectively (Saunders, 1883b).

[2] Hill (1967d: 91), following Waterston (1920a), gave preference to *Secundeisenia* Schulz (1906) over *Pegoscapus* Cameron (1906). According to Ramirez (1970a: 11), the date of publication of Cameron's paper is June 1st, while Schulz (1906: 356) cited *Eiseniella* Ashmead (July 13th, 1906), showing that *Secundeisenia* postdates *Pegoscapus*.

[3] Various genera, now classified with Otitesellini and Sycoecini, omitted.

It may be noted that Saunders, as late as 1883 (a: 11–20; b: v–vi), when he divided Walker's Agaonidae into phytophagous "Sycophagides", and other, presumably parasitic types, classified the former with the Cynipidae. The latter, considered to have "no tribal affinity with *Agaon*", were named "Sycolacides". Westwood, in 1882 as in 1840, allocated *Agaon* to the Chalcididae. The Haplostomata of Saunders, being the group that might prove to be parasitic, were excluded from the Agaonidae by Patton (1884: xvi): "should they prove to be sycophagous the term Sycophagides should be retained for them, as the genus *Sycophaga* is included; otherwise Saunders' term Sycolacides may be employed".

Ashmead (1904a) classified *Agaon* etc. in the nominate subfamily of the Agaonidae; Saunders' Haplostomata, and also *Platyscapa* and *Crossogaster*, formed the subfamily Sycophaginae. Most of the parasitic types were classified in the Torymid subfamily Idarninae; some others in Monodontomerinae (*Physothorax, Plesiostigma;* compare a recent paper by Burks, 1969) or in Miscogasteridae (*Aepocerus;* see Mayr, 1906: 180–181). Ashmead's treatment of the Chalcidoidea set the stage for a long time to come; Schmiedeknecht (1909) duplicated this classification in his volume of the "Genera Insectorum", but considered the Chalcid flies a family instead of a superfamily. In this, Grandi at first followed Schmiedeknecht.

While the fig wasps formed only a small part of the amount treated by Ashmead, Grandi (from 1916 onwards) in an impressive series of major publications, specialized on these smaller groups. He described many species and genera from Africa (1916a, 1917b), Australia (1916b), Ceylon and India (1916c), Java (1917a), the Americas (1919), etc. In so doing, or in separate publications, he provided morphological descriptions of *Blastophaga* (1920a) and *Tetrapus* (1925a), now classified in two subfamilies of the Agaonidae; of *Sycophaga, Apocrypta* (males only) and *Crossogaster* (1916a), *Philotrypesis* (1921b), and *Otitesella* (1922b) — examples of five out of the six tribes now recognized in Sycophagine Torymidae — and *Neosycophila* (1923d), a genus of the subfamily Epichrysomallinae. Thus, except for the tribe Sycoryctini and the subfamilies Toryminae and Eudecatominae, all major types were dealt with! In 1928 (d), Grandi revised the Agaonidae from Mayr's collection, and he published a world catalogue of the group.

In Grandi's opinion, *Sycophaga, Apocrypta* and *Crossogaster* formed the Agaonine tribe Sycophagini (i.e., Saunders' Haplostomata), while the other parasites were part of Ashmead's subfamily Idarninae of the Torymidae (with *Goniogaster* Mayr, the female of *Apocrypta;* see, however, Grandi, 1923d: 113, note). Among the Idarninae, Grandi (e.g., 1925b) distinguished between the "Idarnini veri" and two biological groups containing *Otitesella* and related genera, and *Neosycophila*. Much later (1952a, 1955b), he would again note on these groups, and in 1963 (c) he considered my proposition (Wiebes, 1961b) to include the Sycophaginae with the Idarninae. Anticipating a later discussion of the recent classification of fig wasps, I here include table 4 to provide a synopsis of the larger groups.

Table 4. Classification of fig wasps.

- Agaonidae
    - Agaoninae
    - Blastophaginae
- Torymidae
    - Toryminae (e.g., *Physothorax*)
    - Sycophaginae
        - Sycophagini
        - Apocryptini
        - Sycoryctini
        - Philotrypesini
        - Otitesellini
        - Sycoecini
    - Epichrysomallinae
- Eurytomidae
    - Eudecatominae (e.g., *Sycophila*)

Grandi was particularly interested in the morphological adaptations of insects to special conditions. The various groups of fig wasps and their adaptations were to be compared with the modifications in groups such as mining insect larvae. The *Neosycophila*-wasps, developing in rather superficial galls from which the mature females and males escape directly to the outside, were considered to possess no adaptive deviations from a normal Chalcid morphology. The females of *Otitesella* and related genera too, were considered rather normal. Their males, however, and those of most other groups now classified with the Sycophaginae (Sycoecini excepted), are apterous and also otherwise rather aberrant. The females of most Sycophaginae (not the Otitesellini and Sycoecini) have long ovipositors and in many instances the gaster can be lengthened by telescoping the segments, or the one or two last segments are tubularly lengthened (these characters would later serve as differential characters of several tribes).

The females of the Agaonidae are characterized by the depression of the head; the presence of a facial groove; the reduction of the mouth-parts, although special mandibular appendages are developed; the modification of the proximal antennal segments; the armature of the fore and hind tibiae. (Grandi did not know the function of the pollen pockets.) The males have atrophied mouth-parts; no ocelli; reduced antennae situated in grooves; no wings; etc. Some of these characters were also found with some *Otitesella*-like females (i.e., the modern Sycoecini; not our Otitesellini!) and, in the male sex, also with the "Idarnini veri": Grandi rightly considered these attributes correlated with the way of entering the fig receptacle (females), or with the life within the receptacle (males). For these modifications, which were on several occasions profusely discussed and illustrated (Grandi, 1923a, 1925b, 1929c, 1936c, 1958a, 1959, 1961b), Grandi suggested several ways of origin viz., involutions, rudimentations or disappearance of (parts of) organs, or hypertelic development, displacement, and transformation, and also the development of new (parts of) organs. Some, although always connected with the function the organs have to perform "generally do not seem to be necessary, often not even useful, sometimes even a hindrance (if not disgenic)" (Grandi, 1959: 223). What Grandi seemed to imply is that not all modifications were of apparent importance to the individual or specific existence of the bearer: "e quindi, apparentemente, non vantaggiose alla specie" (1925b: 311). To understand much better, however, the pros and cons of any particular modification (or rather, its function in the composite syndrome in which several modifications coincide), much more would have to be known of the behaviour of the wasps in symbiosis.

Before mention will be made of Grandi's important observations on *Blastophaga psenes* and *Philotrypesis caricae*, which will be the main theme of the next chapter, I shall now discuss the papers by Froggatt (1901) and Pemberton (1921) on Australian *Pleistodontes froggatti*, and by Baker (1913) and Williams (1928) on some Philippine wasps. Actually, Froggatt's paper was not the first on the biology of insects living in figs, and he could refer to several papers on caprification e.g., by Cunningham (1889) on the fertilization of *Ficus roxburghii* (*F. auriculata* Lour.), Howard (1899) and Eisen (1891) on attempts to introduce *Blastophaga psenes* into California as a pollinator for *Ficus carica*. Cunningham described the flowers of *F. auriculata*, and the effects of the presence of insects upon them: he concluded that it is not pollination that causes development, but the irritation following the act of oviposition. The same observation was made by Treub (1902) for *Ficus hirta* of Java, although here some germination of pollen grains was observed. In California, some of the fig growers considered the process of caprification of no practical value, but only the survival of an ancient custom blindly handed down from father to son in Mediterranean regions. Yet, in many places the wasps were successfully introduced (see table 5; Ramirez, 1970b, table 2 listed figs introduced in absence of Agaonidae: they did not set seed).

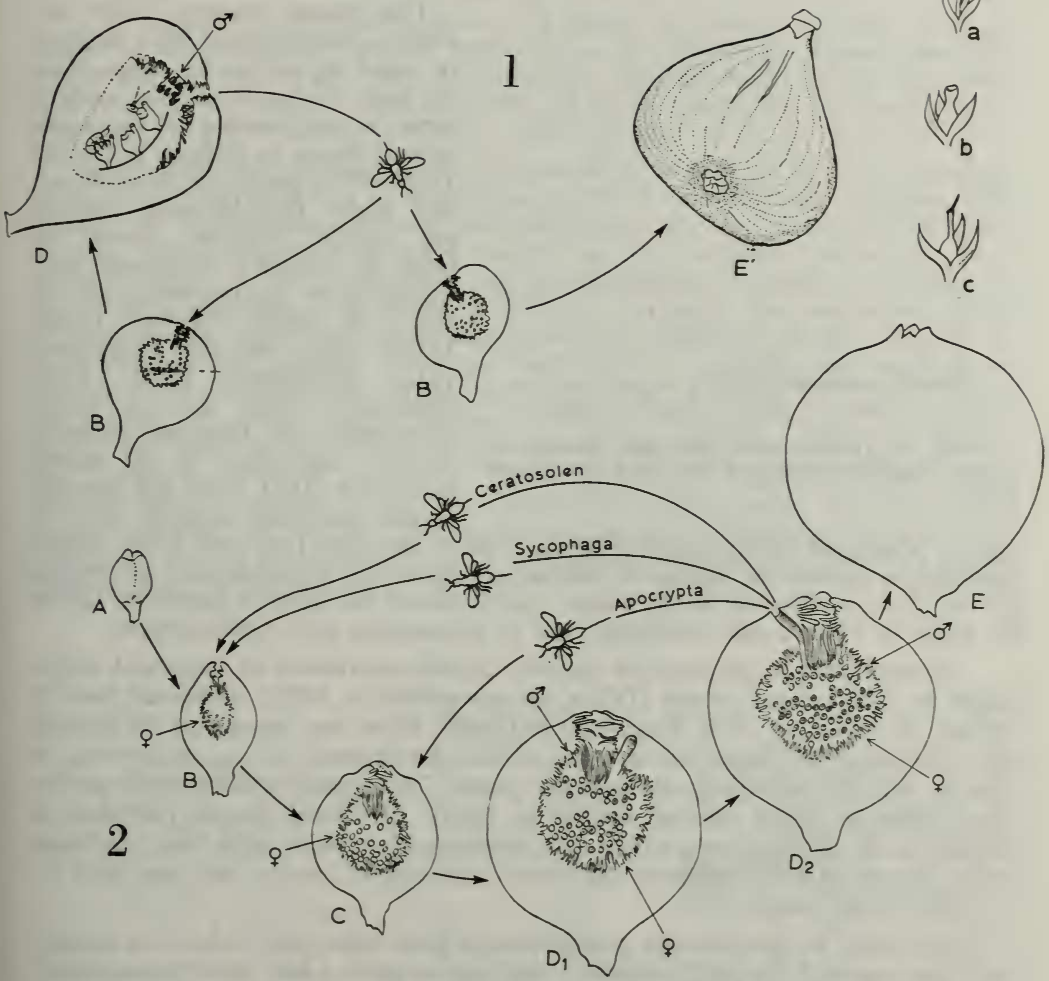
Table 5. Fig wasps introduced with their hosts.

fig	from	pollinator	brought by	introduced to	date	result	selected references
F. carica	? Asia 1)	*Blast. psenes*	? Phoenicians	Mediterranean	? 1400 B.C.	+	Eisen, 1901: 16-20
F. carica	"Asia Minor"	*Blast. psenes*	H.E. Van Deman	California	1890	-	Swingle, 1908: 181
F. carica	Smyrna	*Blast. psenes*	James Shim	California	1891 (twice)	-	Swingle, 1908: 181
F. carica	Smyrna	*Blast. psenes*	Thomas Hall	California	1892	-	Swingle, 1908: 181
F. carica	"Asia Minor"	*Blast. psenes*	A.C. Denotovitch	California	1895	-	Swingle, 1908: 181
F. carica	Naples	*Blast. psenes*	W.T. Swingle	California	1898	-	Swingle, 1899: [8], 1908: 181
F. carica	Algeria	*Blast. psenes*	W.T. Swingle	California	1899	+	Swingle, 1899: [8], 1908: 181
F. carica	?	*Blast. psenes*	?	Australia	?	+	Robson, 1911; Savage, 1924
F. carica	?	*Blast. psenes*	?	Pretoria	?	+	Waterston, 1920a: 128
F. macrophylla	Australia	*P. froggatti*	F.M. [uir]	Hawaii	1921	+	Muir, 1922: 12; Wiebes, 1963b: 307
F. rubiginosa	Australia	*P. imperialis*	?	Hawaii	1922	+	Timberlake, 1923: 200
F. alba	?	[*Blastophaga*]	[Fosberg]	Hawaii	ca. 1930	+	Corner, 1958: 18
F. fistulosa	?	[*Ceratosolen*]	[Fosberg]	Hawaii	ca. 1930	+	Corner, 1958: 18
F. religiosa	East Asia	*B. quadraticeps*	?	Israel	?	+	Galil & Eisikowitch, 1968c: 356

[1] The observation that the entomofauna of the sycones of *Ficus carica* is more complete in India than elsewhere (i.e., it harbours there a species of *Sycoscapteridea* not found in Europe, Mayr, 1885: 153; Joseph, 1957a: 119), adds to the probability of Asia being its homeland.

Ficus macrophylla, the fig observed by Froggatt and Pemberton, is different from the edible fig in that it is monoecious, bearing male, female and gall flowers in one syconium (fig. 2). In other species, male and female flowers occur in separate figs e.g., in *Ficus carica* and *F. nota* (studied by Baker and Williams) (fig. 1; dioecious figs). The entrance of the female *Pleistodontes* wasps through the narrow ostiole of *Ficus macrophylla* was described by Pemberton (1921) as a forward-reaching movement to fix the tips of the hook-like mandibles into the tissue in front and then, in lowering them, to draw the whole body forward over a short distance. The saw-like serrations of the mandibular appendage prevent the head from slipping back. Usually up to five or six wasps will successfully enter a single receptacle, and immediately begin egg-laying. The larva hatching from the egg, matures and pupates within the gall-flower. The wing-less males hatch first out of their galls, and they start in search for a gall containing a female; they fertilize the females by inserting the tip of the abdomen through a hole gnawed in the galls. The females leave the fig by boring a hole through the wall of the receptacle at any point. In doing so they become covered with pollen from the ruptured male flowers which, unlike in many other species of *Ficus* where they are concentrated around the ostiole, are not confined to any particular part of the fig. "Much of this pollen must be brushed from the wasp's body during the short but strenuous trip — to the young fig — , yet sufficient is carried over to secure ample pollination for a great many female flowers" (Pemberton, 1921: 306): it was not noted how the pollen is being transported, and this would remain unknown until 1969!

Many of the details described for *Pleistodontes froggatti* were identically observed for *Ceratosolen notus* and the dioecious *Ficus nota* (see Baker, 1913), and for *Blastophaga psenes* and *Ficus carica* (the former, however, does possess pollen pockets, just as does *P. froggatti*, but these are completely lacking in the latter). Important differences are found in the place where the females leave the receptacle, which is through the ostiole in *Ficus carica* and *F. nota* (where it is often enlarged by the males). Williams (1928: 11–13) listed a number of instances of males enlarging the ostiole or tunnelling close to it. Later we shall learn how important this kind of male behaviour can be.



Figs. 1 & 2. Cycles of dioecious (*Ficus carica*, fig. 1) and monoecious figs (*F. sycomorus*, fig. 2), and their wasps (*Blastophaga* indicated in fig. 1; three with names added in fig. 2). The letters correspond with those used in the text (p. 220); *a*, ♂; *b*, short-styled, and *c*, long-styled ♀ flowers. Adapted from Wiebes (1965a) and Galil & Eisikowitch (1968a).

In comparison with 1882, by 1928 the number of known fig wasps was greatly augmented. For a paper by Van der Vecht (1973), I once computed these numbers of the Agaonidae: they were depicted in a graph reproduced here (fig. 3).

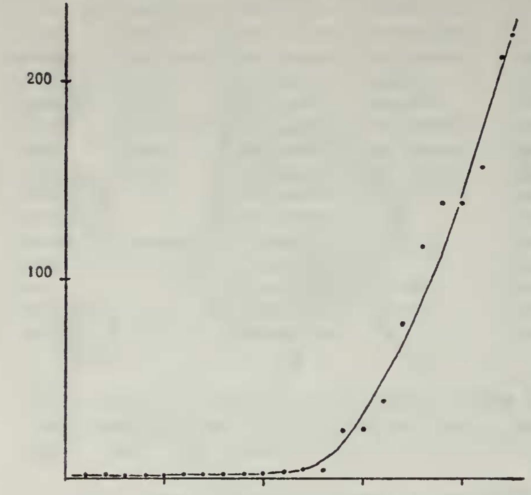


Fig. 3. Trend curve for the number of known Agaonid species. From Van der Vecht (1973).

Waifs and Strays (thirty years of miscellaneous reports)

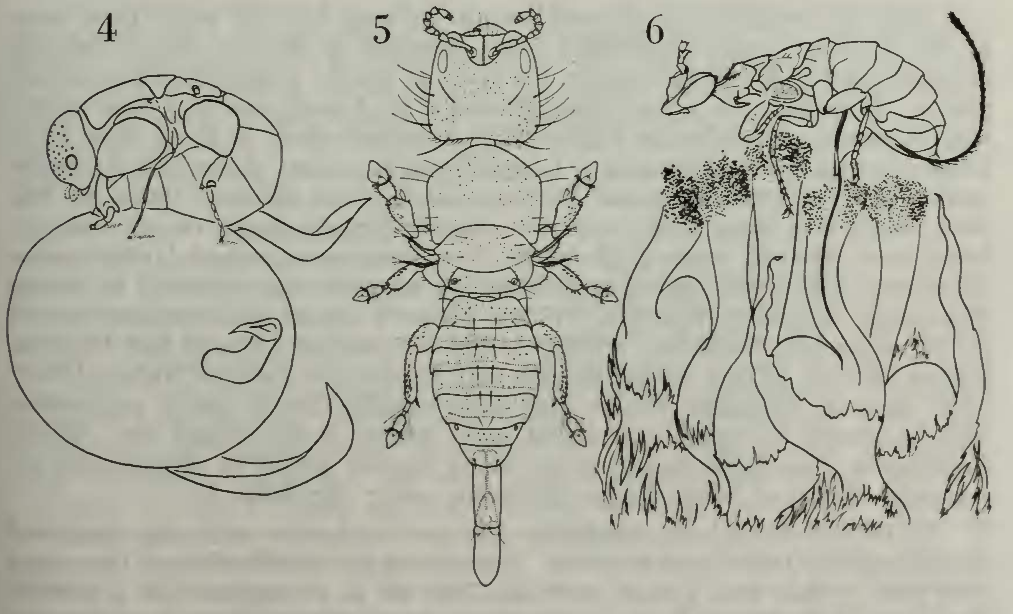
The period between 1928 and 1958 is characterized by a number of small papers on fig wasps from all parts of the world. As such, it forms a continuation of the series already begun by Grandi, Waterston (1914–1921, mainly on new African and some Indo-Malayan forms), etc. Special mention should be made of Grandi's important contributions to the knowledge of the fauna of South America (1934, 1936b, 1938a; see also Hoffmeyer, 1932; Mangabeiro Filho, 1937; Blanchard, 1944) and of Ishii's descriptions of Japanese parasites (1934). Also some of the papers by Girault (1913–1939) fall into this period, and they certainly may be named waifs and strays (see De Santis, 1961)! Between 1951 and 1957, Risbec published a number of papers on African and Malagasy Chalcidoidea; see Wiebes (1970a) for a revision of the fig wasps. Joseph started his series of papers on Indian fig wasps in 1952; it was concluded later in cooperation with Abdurahiman.

As mentioned in the previous chapter, Grandi contributed an important monograph on *Blastophaga psenes* (1920a, second edition in 1929a, additional note in 1935a). In 1936 and 1938, Buscalioni & Grandi wrote two papers on the biology and cultivation of *Ficus carica,* and on the development of its receptacles, in relation with the pollinator *Blastophaga psenes.* The parasite *Philotrypesis caricae* was treated in 1921b (second edition in 1930). In 1961b, Grandi published in English on his findings; some of the data mentioned here were taken from that summary. Joseph (1958) combined additional notes on *B. psenes* and new data on *P. carica,* in his thesis.

The males of *Blastophaga psenes* emerge from their galls before the females do. They approach the galls containing the females, gnaw a hole with the mandibles, introduce the tubularly lengthened last segments of the gaster, and fertilize the females while they are still in their galls (fig. 4). Each male copulates with several females (the sex ratio is 9–18 males for 100 females), and dies within the cavity of the fig. The females, after having left their gall through the hole made by the male, on their way to the ostiole pass the region of the male flowers where they become dusted with pollen. The scales of the ostiole of the D-phase fig (see fig. 1) easily yield and allow the females a passage out. The scales lining the ostiole of the B-phase figs, where the females now go, offer more resistance: the wasp wedges its head under the free edge of the outer scales, then goes on laboriously through the scales and in this process, looses its wings and parts of the antennae and legs. The number of females found in the cavity of the young figs seems to vary e.g., Condit (1918: 539) mentioned eighteen, Grandi (1929a: 109) found no more than four. In the cavity of a gall-fig (see fig. 1), the female may oviposit in as many as 300–400 flowers (in the ovary, between the nucellus and the integument); for some variation. see Grandi (1929a: 113). At the same time a small quantity of fluid from the acid gland is injected into the endosperm, causing its proliferation into nourishing tissue for the wasp larva. The larva passes through two larval stages and a prepupa before the pupal stage; complete development takes two-and-a-half, two, or seven months, depending on the generation falling in spring, summer, or winter, respectively (on the number of generations, see Joseph, 1958: 212–216).

The actions of the females inside the edible or (young) seed-figs are very similar to those described above; however, as the long-styled flowers have the ovaries out of reach of the wasp ovipositor, the females finally perish after their futile attempts to perpuate the species but not before pollination has been accomplished (see a good account in Condit, 1947: 42–46).

After considering all facts, wrote Buscalioni & Grandi (1936: 117; translated from Italian): the symbiosis of *Blastophaga* and our *Ficus* is rather complex, and, through the intervention of Man, has developed into an association of three partners. The *Blastophaga* and the caprifig can be explained exclusively as a parasitic action on the ovules; Man, by practising deceit ("mercé un inganno"), succeeded in exploiting the insect, compelling it to enter the receptacles of the domestic fig, the flowers of which, long-styled by cultivation, escape infection by the insect [end of citation]. It is true that there is a complicated sequence of different types of receptacles on the wild fig tree viz., a winter form with mainly gall flowers and some male; a summer form with a mixture of gall and female flowers, or with female flowers only; and an autumn form with gall flowers only, in which the wasps overwinter. Without entering a further discussion here, I suggest there is nothing in which the symbiosis of *Ficus carica* and *Blastophaga psenes* fundamentally differs from symbioses of other dioecious figs and their pollinators. As will be shown below, in comparison with many, it even is a rather simple instance of mutualistic symbiosis.



Figs. 4–6. Three figures of great historical interest: 4, *Blastophaga psenes*, male mating with female in gall; 5, *Philotrypesis caricae*, male; 6, *Ceratosolen arabicus*, female ovipositing and pollinating. From Grandi (1920a, 1921b) and Galil & Eisikowitch (1969a).

The generations of *Philotrypesis caricae* are much the same as in *Blastophaga psenes.* The following account is for a great part taken from Joseph (1966: 401-402). Copulation of males and females mostly takes place outside the gall, soon after the female is liberated by the male from the ovary in which it developed. A single male copulates with several females (sex ratio, 50–60 males for 100 females). The oviposition will be discussed in the next chapter; about fifty eggs are laid by a single female. It seems that the factor determining the oviposition is the presence of the acid secreted by the *Blastophaga.* At the beginning, the larva of both *Blastophaga* and *Philotrypesis* feed on the endosperm, but later the *Blastophaga* is starved by the *Philotrypesis* — or may be weakened by some toxic secretion produced by the *Philotrypesis.* This explains much of the unisexual variation in size of the imagines, as the quantity of food left for the *Philotrypesis*-larva depends on whether the *Blastophaga* is being killed early or late in the second instar. This may also influence the sex ratio: it has been suggested that haploid males are able better to survive partial larval starvation than do diploid females.

Wasps in Symbiosis (the period after Joseph, 1958)

In my opinion, Joseph's doctor's thesis (Joseph, 1958), discussed in the previous chapter, opened a new period in the history of fig wasp research. Joseph knew the edible fig and its symbionts as well as Grandi did, but he moreover gained an intimate knowledge of the biology of the tropical forms and their parasites. Many proved new to science, and thus it took Joseph, as it later did also me as well as Hill and Ramirez, much time to describe the new genera and species: a task still unaccomplished. Gradually, however, a new classification of fig wasps arises, enabling a comparison of the classification of *Ficus* and the underlying hypotheses (Corner, 1965, 1967–1975) with the phylogenetic classification of the wasps.

THE POLLINATORS

Soon, the specificity of the relationships between figs and wasps (here taken in the restricted sense: Agaonidae only) appeared to be very strict. This was already surmised by Grandi earlier, but it could not be proved before a botanist and an entomologist, in a joint effort, studied a great many species. Corner started this cooperation with Van der Vecht (1959; collections made in Java), from whom I took over the entomological part. I started with a revision of the Indo-Australian species of *Ceratosolen* Mayr and *Pleistodontes* Saunders (Wiebes, 1963a, b). Hill, who collected in Hong Kong, and later also in Uganda, began on a revision of Hong Kong figs and wasps (Hill, 1967a, b, d), and monographed *Liporrhopalum* Waterston (Hill, 1969). Ramirez collected fig wasps in the Americas; he revised *Pegoscapus* Cameron (Ramirez, 1970a). Later, I would add revisions of the genera *Alfonsiella* Waterston (Wiebes, 1972b), *Elisabethiella* Grandi and *Nigeriella* Wiebes (Wiebes, 1974a), *Agaon* Dalman and *Allotriozoon* Grandi (Wiebes, 1974c), while those of *Deilagaon* Wiebes and *Waterstoniella* Grandi are in preparation. This, it should be noted, still leaves large groups to be revised e.g., African *Ceratosolen, Eupristina* Saunders, the many species united in *Blastophaga* s.l., American *Tetrapus* Mayr. Large collections exist: see table 6.

In 1973, I divided the Agaonidae into two subfamilies viz., Agaoninae and Blastophaginae; later again in 1974a, I compared the classification of the genera with that of their host groups of *Ficus.* This led to a suggestion of a possible classification of the figs into a number of groups different from those used by Corner (1965) but coinciding with the (supposedly phylogenetic) groups of the wasps (see table 8). One example will be discussed at the end of this chapter.

Table 6. Important collections of fig wasps made since 1950.

provenance	collector	*Ficus* by	some references
Asia, Australasia	Corner	Corner	Corner, 1958, 1963c
"	Bishop Museum	-	Wiebes, 1976
India	Joseph	Joseph	Joseph, 1952 ff.
Indonesia, mainly Java	Van der Vecht	Corner	Wiebes, 1961b ff.
N. Borneo (Kinabalu)	Corner	Corner	Corner, 1964
Philippine Is.	Wiebes & Pancho	Corner	Wiebes, 1965a, 1974d
"	Noona Dan	-	Petersen, 1966
Hong Kong	Hill	Hill	Hill, 1967a, d
Solomon Is.	Corner	Corner	Corner, 1967
"	Noona Dan	-	Petersen, 1966
Malagasy	Blommers	Blommers	Wiebes, 1974c
La Réunion	Etienne	Cadet	-
East Africa	Galil	Galil	Wiebes, 1964b, 1968a
Uganda	Hill	Hill	Wiebes, 1972b, 1974c
Guinea (W. Africa)	Lamotte & Roy	-	Joseph, 1959a
Nigeria	Medler	Mrs. Medler	Wiebes, 1972a ff.
Central America	Ramirez	Ramirez	Ramirez, 1970a
"	Ramirez, Gordh	Ramirez, Gordh	Gordh, 1975

Ramirez (1974) took another course, basing himself on the same old table (Wiebes, 1963a: 101, table 2) and host catalogue (Wiebes, 1966b) as revised later by Hill (1967c: 427, table), but he added an interesting discussion of many concurrent characters of Agaonid genera and *Ficus*-subgenera and sections. This new approach became possible, as new data were known on the biology of figs and wasps.

As usual in biology for too long a time, the one instance of *Blastophaga psenes* and *Ficus carica* taken from the temperate region, was considered to present a good example of the symbiosis of figs and wasps in general. The situation in the edible fig, however, appeared to be quite simple compared to the pollination process in several tropical species. In *Blastophaga psenes*, the pollen is passively carried on the body of the female wasp ("topocentric pollination" *sensu* Galil, 1973a). As Galil and his coworkers, in many papers of very high standard from 1965 onwards, have shown, the situation is not always as simple in other *Ficus* species, where "ethodynamic pollination" may occur. There proved to be a considerable variation in structure and behaviour of the pollinators of different species of *Ficus*. Unique organs used as containers by various species of wasp, for transporting pollen from male figs to young receptive female figs (c.f. fig. 6), were independently but almost simultaneously, recorded by Ramirez (7.ii.1969, "corbiculae"), Galil & Eisikowitch (9.v.1969, "pollen pockets"), and Chopra & Kaur (3.vi.1969, "pollen stuck to the epimeral region of the mesothorax"). In common consent of Galil, Ramirez, and Eisikowitch (1973: 176, note), the name "corbiculae" is used for the pollen-carrying organs on the fore coxae ("coxal corbiculae" *sensu* Ramirez), while for the more complicated thoracal organs the term "pockets" is used ("sternal corbiculae" *sensu* Ramirez). In spite of numerous structural differences between the syconia of dioecious and monoecious figs, the two may have several biological features in common (Galil, 1973b: 309). In table 7 I list the species of fig and pollinator on which we have information concerning the pollination process (except for some discussed above), with the literature-references added. As in previous sections, in the following compilation of what is known on fig-wasp behaviour in various figs, some important parts are verbally taken from the original reports.

Table 7. Pollination and/or oviposition behaviour described for monoecious (m) and dioecious figs (d).

UROSTIGMA	pollinator	references
Ficus macrophylla (m)	*Pleistodontes froggatti*	Froggatt, 1901; Pemberton, 1921
Ficus religiosa (m)	*Blastophaga quadraticeps*	Galil & Eisikowitch, 1965, 1968c, 1971; Galil & Snitzer-Pasternak, 1970; Galil, Zeroni & Bar Shalom, 1973; see also Johri & Konar, 1956
Ficus costaricana (m)	*Pegoscapus estherae* 1)	Galil, Ramirez & Eisikowitch, 1973
Ficus hemsleyana (m)	*Pegoscapus tonduzi*	Galil, Ramirez & Eisikowitch, 1973
PHARMACOSYCEA		
Ficus spp. (m)	*Tetrapus* spp.	Ramirez, 1970a
FICUS		
Ficus carica (d)	*Blastophaga psenes*	Grandi, 1920a, 1929a; Joseph, 1958
Ficus hirta (d)	*Blastophaga javana*	Treub, 1902
Ficus auriculata (d)	*Ceratosolen emarginatus*	Cunningham, 1889 2)
Ficus nota (d)	*Ceratosolen notus*	Baker, 1913; Williams, 1928
Ficus hispida (d)	*Ceratosolen s. solmsi*	Lee & Tan, 1973
Ficus fistulosa	*Ceratosolen hewitti*	Galil, 1973b
SYCOMORUS		
Ficus racemosa (m)	*Ceratosolen fusciceps*	Chopra & Kaur, 1969 3)
Ficus sycomorus (m)	*Ceratosolen arabicus*	Galil, 1966; Galil & Eisikowitch, 1968a, b, 1969a, 1971, 1974

[1] See Ramirez (1970a) for further details on *Pegoscapus*-behaviour.

[2] I am not sure that Cunningham's observations refer to this species of wasp.

[3] *Ficus tsiela* with *Maniella delhiensis, Ficus virens* with *Blastophaga vaidi* [sic!], and *Ficus carica* with *Blastophaga psenes* were also mentioned but no details were given.

Galil & Eisikowitch (1968a: 262-265, fig. 6) distinguished between the developmental phases of *Ficus sycomorus* as follows (see fig. 2):

Phase A (*pre-female*). — young syconium prior to the opening of the ostiole.

Phase B (*female*). — ostiolar scales loosen, female flowers ripen, sycophilous wasps penetrate into the syconium and oviposit into the ovaries; pollination of the female flowers.

Phase C (*inter-floral*). — wasp larvae and fig embryo's develop within their respective ovaries; ovaries occupied by the larvae are transformed into galls.

Phase D (*male*). — male flowers mature, wasps reach the imago stage, fertilized female wasps leave the syconia via channels bored by the males.

Phase E (*post-floral*). — both the syconia and the seeds inside them ripen.

Ceratosolen arabicus and the monoecious Ficus sycomorus (see Galil & Eisikowitch, 1968a, b, 1969a, b, 1974). — In two phases viz., the female phase B and the male phase D, the sycophilous wasps are active within the syconium. In the last-mentioned male phase, the male flowers at first remain closed, while the male wasps emerge from their galls, puncture the walls of the female galls and impregnate the females within. Then, the males assemble at the upper part of the syconium: at the end of the first day, the amount of liquid in the syconium decreases and the stamens gradually protrude from their perianths at the male zone of the fig around the ostiole.

In the morning of the second day, the male wasps start working at the male flower zone: they clasp the anthers and tumble down into the cavity of the fig while still holding the anthers between the legs. At the same time, the female wasps start to emerge from their galls, they approach the cut anthers and grasp them. With the mandibles and with the scapes of the antennae, a female widens the narrow dehiscence slit of the anther, and with the arolia of the fore leg lifts pollen on to the ventral surface of the body. Then, the wasp curves the thorax so that the covering membranes of the pollen pockets stand out along their inner suture: a wide opening now leads into the pocket. The pollen is shoveled into the pocket with the combs of the fore coxae.

In the mean time, the males have made tunnels, one to three per syconium, in the male flower zone close to the ostiole. Through these tunnels, the females eventually emerge, their pockets loaded with pollen.

The pollination act in *Ficus sycomorus* is here described after Galil & Eisikowitch (1969a), while some details were taken from their 1974 paper. Immediately upon entering the young syconia at the female phase (B), the female of *Ceratosolen arabicus* starts ovipositing into the pistils, one after the other. Toward the end of the oviposition, the fore legs of the wasp fold back until the arolia reach the lower margin of the pockets (fig. 6). Then, the tarsi touch the stigmata below, and so bring the pollen grains on them.

Ceratosolen hewitti and the dioecious Ficus fistulosa (see Galil, 1973b). —— Here the wasp-releasing D-phase male figs and receptive B-phase figs of both sexes grow on different trees. The behaviour in the D-phase does not differ essentially from that of *C. arabicus* in *F. sycomorus.* Also the behaviour of the females on the short- and long-styled female flowers (in different figs) is almost identical, although eggs are not likely to be laid through the long-styled pistils of the female flowers.

Blastophaga quadraticeps and the monoecious Ficus religiosa (see Galil & Eisikowitch, 1965, 1968c; Galil & Snitzer-Pasternak, 1970, 1971; Galil, Zeroni & Bar Shalom, 1973). —— The behaviour of the wasps is somewhat different from that in *Ceratosolen arabicus* in that the males, after the copulation act, do not cut the anthers as the *Ceratosolen*-wasps do. The fertilized females remain in their galls for many hours. In the mean time, the males bore the exit holes, and only afterwards do the females begin to emerge. In a series of beautiful experiments, Galil and coworkers proved that it is the replenishment of the internal atmosphere by air from outside the syconium — lowering the CO_2-content to less than 3-4 percent — that enables the females to leave their galls. At the same time, this lower CO_2-content inactivies the male wasps. The diagram of fig. 7 illustrates the reciprocal relationships (after Galil, Zeroni & Bar Shalom, 1973: 1122, fig. 7).

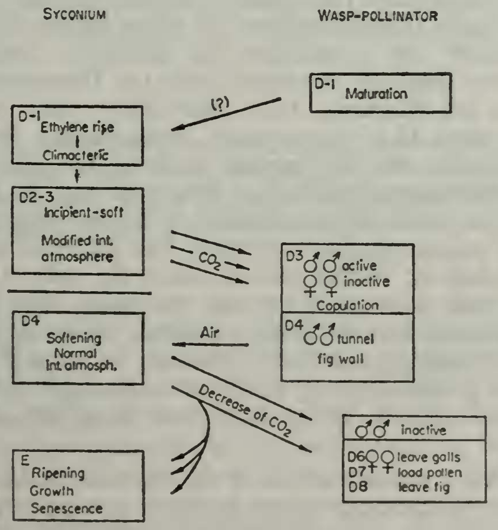


Fig. 7. Reciprocal relationships between the fig and the pollinator in *Ficus religiosa.* From Galil, Zeroni & Bar Shalom (1973).

Now, the females approach the still intact anthers and — here as in *Ceratosolen arabicus,* with the antennal scapes and the mandibles — crumble the pollen. The fore tarsi touch the anthers, and the pollen pockets are loaded. Also the unloading of the pollen and the act of pollination, in the B-phase young figs, are the same for *Blastophaga quadraticeps* and *Ceratosolen arabicus.*

Pegoscapus tonduzi (and *P. estherae*) *and the monoecious Ficus hemsleyana* (and *F. costaricana*) (see Galil, Ramirez & Eisikowitch, 1973) —— The wasps of most species of the genus *Pegoscapus* do not have thoracal pollen pockets only, but coxal corbiculae as well. As in *Ficus religiosa,* the female wasp after leaving its gall, approaches the male flower and pushes its head between the pistils in search for open anthers. The flagella of the antennae are pressed into the anther, while the scapes keep open the dehiscence slit. In these species again, the pollen is taken with the fore arolia and brought on the mesosternum, where the pollen pockets not being completely covered as in the previously mentioned species, receive the pollen as it is shoveled in with the coxal comb. Also the coxal corbiculae act as pollen containers during the transport to a young fig, after the females have left the D-phase syconium through exit holes gnawed by the males.

The pollination act by *P. estherae* was divided by Galil, Ramirez & Eisikowitch, into the following steps. 1, preparatory step: oviposition; 2, combing of pollen from pockets to corbiculae: pollination now starts; 3, transfer of pollen from coxal corbiculae to the arolia of the fore legs; and 4, pollination proper: the striking of the fore tarsi on each other, and shaking off the pollen on the stigmata below.

I discussed the data on pollination in *Ficus* at some length, because they are of the greatest interest for the understanding of the symbiosis of figs and wasps. Hopefully, this compilation will stimulate further research and completion of our, as yet very incomplete, knowledge of the situation in many groups: "so as to obtain a broader view of the evolution of the interrelations between the figs and their pollinating wasps" (Galil, Ramirez & Eisikowitch, 1973: 183).

At this time, the taxonomic implications are not yet very clear. On the one hand, the shape and structure of some of the organs used in emerging from the galls, pollination within figs, or in entering the young syconia, were used for the distinction of the two subfamilies of the Agaonidae (Wiebes, 1973) viz., the elongate head and the subvertical orientation of the female mandible (Agaoninae); the ventral crenulations (Agaoninae) or ridges (Blastophaginae) on the mandibular appendage, which is rigidly (Blastophaginae) or rather loosely connected (Agaoninae) to the mandible proper; the prominent and articulate elongation of the third antennal segment, more distinctly developed with the Blastophaginae than with the Agaoninae; etc. (but see Ramirez, 1974, who finds other connections). On the other hand, in one genus (e.g., *Pegoscapus, Pleistodontes, Waterstoniella*) pollen pockets and/or corbiculae may be present in some but absent in other species, indicating that a resemblance in pollination behaviour may be the result of convergent evolution. *Tetrapus* seems to be primitive in several aspects (Ramirez, *in litt.*) e.g., it lacks external pollen-carrying structures (the pollen is eaten, and carried in the digestive tract; Ramirez, 1970b), and it also is the only Agaonid not breaking wings and antennae while entering the young syconium. Also in *Pleistodontes,* the condition without pockets may well be primitive, while their presence (e.g., in *P. froggatti, imperialis*) may be a derived character. In some of the Blastophaginae, however, the external pollen-carrying structures seem to be secondarily lost (e.g., in some *Waterstoniella*), or are in the process of being lost (as in *Waterstoniella masii*).

What is needed for a reconstruction of the coevolution of figs and wasps, is a more complete survey of character-states in many groups, permitting of a phylogenetic analysis. The groups to be prospected include all symbionts of the fig, inquilines and parasites (in short: mess-mates) as well as pollinators. The symbioses, then, are taken as the taxonomic units of the phylogenetic classification, while the wasps (with all their features) are treated as the characters of the symbiosis. Although some classification on the tribal level was recently suggested, and accepted by students of fig insects (see table 4), the knowledge of the mess-mates is as yet very scanty[1]). A survey of some, mostly biological data is presented below.

THE MESS-MATES

Agaonidae

The symbioses of figs and wasps have other partners than pollinators and plants. Recently, it became known that some of the Agaonidae behave as cuckoos: laying eggs without preparing food (i.e., pollinating the flowers!). The first and best known instance is *Ceratosolen galili* in *Ficus sycomorus* (see Wiebes, 1964b, 1968a; Galil & Eisikowitch, 1968a, 1969a). The female has pollen pockets and its behaviour during oviposition is quite similar to that of *Ceratosolen arabicus:* the pockets are always empty, however, and pollination movements have not been observed. In a way, its behaviour is similar to that of *Sycophaga sycomori* (at least, its place in the symbiosis is). In my opinion, *C. galili* is not closely related to *C. arabicus.* This poses the question as to the evolution of its relationship with the sycomore fig. As seen from its pollen pockets, *C. galili* in a previous evolutionary stage acted as a pollinator, but to which fig? If it is conceivable that two species of fig merge, keeping one of the pollinators as such while the other is lost or develops into a food-parasite; or that a species of wasp switches from its "own" fig to another, to act as a parasite — what about the supposed phylogenetic specificity of figs and wasps?

Several instances of supposed parasitic Agaonidae are now known, mainly from Africa. A previously recorded case of an Indo-Malayan fig harbouring two Agaonidae (Wiebes, 1966c) should be reconsidered in the light of our new knowledge. Also the instance of two species of *Pegoscapus*-symbionts of *Ficus tuerckheimii* in Costa Rica (Ramirez, 1970a) should be reinvestigated. Some more species of *Ceratosolen* seem to belong to the group of *C. galili* e.g., *flabellatus,* which lives in the syconia of *Ficus capensis* next to what I suppose to be the legitimate partner (*C. capensis*). Some species of *Alfonsiella* are sometimes found in figs evidently pollinated by other wasps (i.e., *Elisabethiella;* Wiebes, 1972b): a male of *Alfonsiella* was found next to one of *Elisabethiella* in *Ficus salicifolia* by Mayr (1885: 192), and it was mistaken for an apterous form of *Crossogaster triformis* (see Grandi, 1928d: 206-210; Wiebes, 1975). More often than not, however, the species of *Alfonsiella* are found quite alone, and they do have pollen pockets.

Toryminae

Physothorax, from figs of section *Americana,* was recently recognized as one of the Toryminae (Burks, 1969). The females have long ovipositors, with which they pierce the fig receptacle from the outside (Butcher, 1964: 237). There are winged as well as wingless (or brachypterous) males.

Sycophagini

Sycophaga sycomori is one of the Sycophagini, a tribe of the Torymidae Sycophaginae (see table 4). *Sycophaga* contains a number of species all of which, as far as known or assumed from their morphology, enter the figs of African *Sycomorus* through the ostiole to oviposit. *S. sycomori* is able to induce the formation of parthenogenetic nourishing tissue for its larva. This tissue, however, originates in the nucellus and not in the endosperm as in *Ficus carica* (see references in Grandi, 1929a: 112) or in *Ficus religiosa* (Johri & Konar, 1956).

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[1] Hill (1967d: 95) listed ten genera as "incertae sedis". Some of these were mentioned above (*viz.*, nos. 1, 2, 6, 7, 8, 9): which leaves only four unplaced *viz.*, *Critogaster* Mayr (American parasites of *Tetrapus*), *Dynatogmus* Mayr from Africa, *Heterandrium* Mayr (American parasites of *Pegoscapus*) and *Pseudidarnes* Girault from Australian *Malvanthera*.

The behaviour of *Sycophaga sycomori*, and its effects on the structure and development of *Ficus sycomorus*, were discussed by Galil, Dulberger & Rosen (1970; see also the papers by Galil & Eisikowitch mentioned with *F. sycomorus*, above).

The females of most Sycophagini have long ovipositors, and they oviposit from the outside of the fig, through the peel. Ansari (1966: 80-82, *Parakoebelea*; 1967: 380-381, "*Idarnes*") described the process of egg-laying in Sycophagine wasps (see fig. 8a, b). After locating a proper place on the surface of the fig, the female moves forward in order to bring the distal end of the ovipositor near the selected place. Holding the fig firmly with its legs, the female moves its ovipositor forward and backward till the surface of the fig is punctured; then, the insect creeps backward, pushing the ovipositor (guided by the valves, from which it gradually dislodges proximally) into the fig receptacle. Usually, one egg is deposited into each gall flower, but in some cases two eggs were laid: it is worth mentioning that Ansari recorded the finding of two specimens viz., a male and a female developing within a single gall — in my opinion, this record wants confirmation. The males of the Sycophagini are rather aberrant. Grandi (1916a: 227-228, figs. 32, 1; 36, 2; etc.) described the peculiar transverse division of the head into two parts, the anterior of which bears the eyes, the antennae, and the sockets for the mandibular condyles. The gaster bears very long, laminate excrescences of the spiracles of the eighth urotergite. The morphology of the male *Idarnes* (*Ganosoma* in Mayr's sense) recently redescribed by Gordh (1975: 408-412), shows that its relationship to the Old World Sycophagini cannot be very close as e.g., the head is relatively normal, and the spiracles of the eighth urotergite have no excrescences.

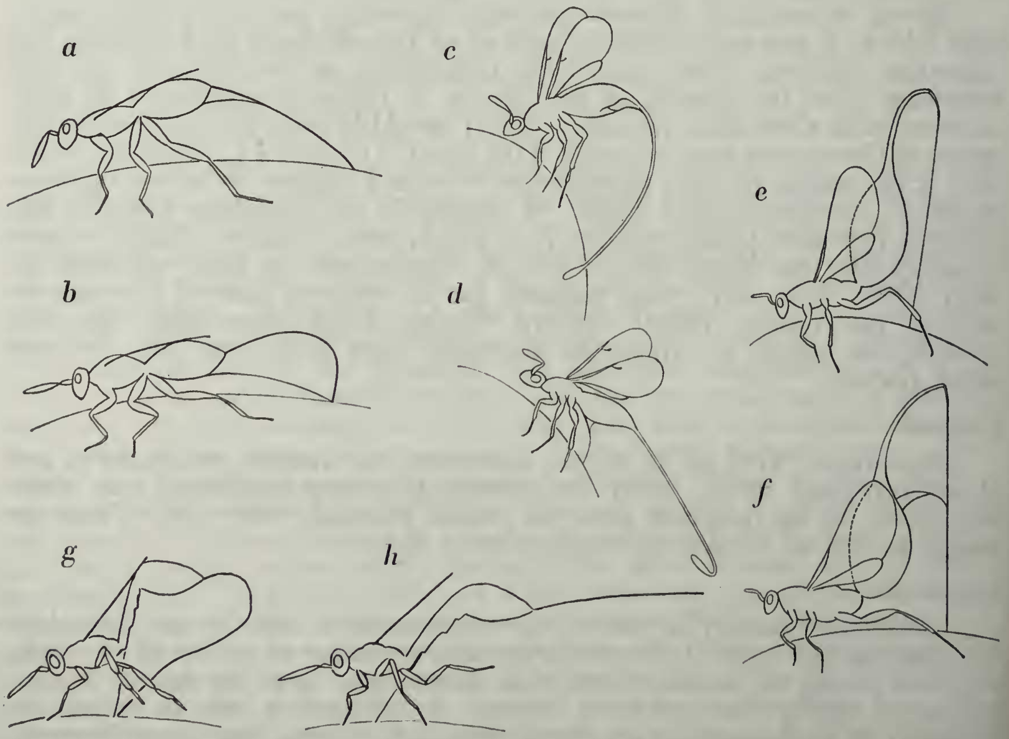

Fig. 8. Some stages in the process of oviposition in Sycophagini (*a*, *b*), Sycoryctini (*c*, *d*), Philotrypesini (*e*, *f*), and Apocryptini (*g*, *h*). Adapted from Joseph (1953a, 1958) and Ansari (1966, 1967).

Ansari used the term "cleptoparasite" for the wasps discussed, and Hill (1967c: 431) suggested that the species of *Eukoebelea* are phytophagous and compete with the Agaonidae for the ovule endosperm. In young receptacles of

Ficus nota in the Philippines, I saw *Eukoebelea* ovipositing (? no eggs observed!) before *Ceratosolen* had entered the fig.

Eukoebelea has been recorded from sections *Neomorphe* and *Sycocarpus*, and from subgenus *Sycomorus* (see the plant groups mentioned in table 8); the genus *Idarnes* is restricted to section *Americana* (see Gordh, 1975), while the Old World species alluded to this group have a rather wide host-spectrum; *Parakoebelea* is known from Indian and African *Sycomorus* (and one species from section *Conosycea*?); while *Sycophaga* only occurs in African *Sycomorus*. In general, most Sycophagini ("*Idarnes*" excluded) appear to be living in figs pollinated by Agaonidae of the genus *Ceratosolen*, and by those of *Pegoscapus*.

Apocryptini

Again, reference should be made to the paper by Ansari (1967). *Apocrypta westwoodi*, like all congeners, is peculiar in having the female gastral segments keeled, permitting of a telescoping lengthening of the gaster. The insect, in drilling a hole through the peel of the fig, raises its hind pair of legs, and the ovipositor is pushed in, beneath the body of the wasp (fig. 8g). The ovipositor gets lodged in the grooves formed by the gastral sternites. Now the legs are relaxed; the valves still guide the ovipositor until, after thrusting a considerable length of the ovipositor, the wasp suddenly pulls out the valves, which now rest over the fig or swish in the air (fig. 8h). The male (Grandi, 1916a: 264-273) is slender, and has large — although never protruding — spiracular peritremata of the eighth urotergite.

The species seem to be restricted to *Ceratosolen*-harbouring figs viz., *Neomorphe, Sycocarpus* and *Sycomorus*. Presumably, *A. longitarsus* parasitizes (or lives as an inquiline with) *Sycophaga sycomori* in Israeli *Ficus sycomorus* (Galil & Eisikowitch, 1968b: 757). It is peculiar, and well worth further research, that some related forms from African figs are much larger and more robust, in the same relation to normal *Apocrypta* as *Parakoebelea* stands to *Eukoebelea*.

Sycoryctini

The Sycoryctini form a large tribe, the internal relationships of which are not very clear. In the Sycoryctini, the apparent gaster ends with the eighth urotergite, and the ninth is tubularly lengthened covering the valvulae almost to the tips (forming a "tail"). Joseph (1953c: 67–69) described the process of oviposition for *Sycoscapteridea* (fig. 8c, d). When the female feels a particular spot to be suitable, the tip of the "tail" is brought in contact with the surface, which is pierced. As the insect creeps backward, the ovipositor, dislodged from the sheathing "tail", is thrust into the fig. After oviposition, the wasp pulls out the ovipositor in an interesting manner: it slowly raises the gaster by straightening its bent legs and gently pulls out the ovipositor stage by stage, while slowly creeping forward till the whole ovipositor is out of the fig. The males are less depressed or slender than in the Sycophagini or Apocryptini, respectively; the head is not divided into two parts, and the spiracular peritremata are not prominent, nor very large.

The Indo-Australian genera were keyed by Wiebes (1967e: 173). They are generally found throughout the subgenera *Urostigma* and *Pharmacosycea* (both, Old World species only), and *Ficus*, but not occurring in all species. Hill (1967c: 431) noted that they may well be parasites of the Agaonidae or even of the other Sycophaginae, as they are noticeable smaller than the other wasps in their respective fig faunas.

Philotrypesini

The cleptoparasite of *Blastophaga psenes* in *Ficus carica* is a member of this tribe; its oviposition-behaviour was studied by Joseph (1958) while earlier observations, with a figure of ovipositing female wasps, were given by Lichtenstein (1919, figs. 2–3). With the females of the Philotrypesini, the eighth and ninth gastral segments are modified, and they form part of a "tail"; moreover, the ovipositor proper and its valves are rather long. Here again, as in the Apocryptini, the gaster is raised high, and the wall of the fig is pierced almost beneath the body of the wasp (fig. 8e, f). Then, the ovipositor is dislodged from its sheath. According to Joseph (1958: 225), the valves remain at the point of insertion of the ovipositor, and they are not kept backward as Lichtenstein (1919: 316) recorded; only in case of disturbance, the valves are kept "en position de repos". The males of *Philotrypesis* (fig. 5) show some superficial resemblance to those of the Sycoryctini, but they may — among other things — be easily distinguished by the emarginate ventral stomal edge. Some species have fully winged ("homomorphic") males, and several intermediate forms may occur in one sample (for these and other variations, see Grandi, 1930: 53-71).

The species occur in Old World groups of *Urostigma, Oreosycea* and *Ficus. Sycomorus* has no *Philotrypesis.*

Otitesellini

The females have a short ovipositor, and for that reason are supposed to oviposit from within the fig receptacle. Some have special features evidently related to the way of entering the fig e.g., rasp-like regions on the thorax (*Eujacobsonia*), stout teeth or spines on the legs (*Grasseiana, Lipothymus*), etc. The males are peculiar by their oversized heads and mandibles, and they superficially resemble those of *Philotrypesis.* The hosts are found in the Old World groups of *Urostigma* (*Malvanthera* excluded), *Oreosycea*, in a few species of *Sycidium*, and one of *Sycocarpus.* For a review, see Wiebes (1974d: 161).

Sycoecini

Several of these were formerly classified with the Sycophaginae in the old sense, until Hill (1967d: 94–95, 98) erected a separate tribe for their reception. The females have several adaptations for penetrating the fig ostiole, especially in various appendages to the mandibles or the fore tibiae (see also the remarks on *Seres*, by Ramirez, 1974: 774, 776). The males are alate. The distribution of the group is disjunct, one genus (*Diaziella,* see Wiebes, 1974b) occurring in the Philippines (presumably in some figs of section *Conosycea*), while all others are African (host figs of section *Galoglychia,* and one in section *Urostigma*).

Epichrysomallinae

Several genera, some of which with a complicated taxonomic history having been classified with several Chalcidoid families, were recently united in this subfamily (see Hill, 1967d: 96–98). Since then, three new genera were added viz., *Parasycobia* and *Sycobiomorphella* by Abdurahiman & Joseph (1967b), and *Sycophilomorpha* by Joseph & Abdurahiman (1969). The species occur mostly in *Urostigma*-figs, but one was recorded from *Ficus ampelas*, another from *F. tinctoria* (both, section *Sycidium*): it is on these that some biological data are available. Females and males of *Neosycophila omeomorpha* Grandi (see 1923d), both fully winged, develop in large galls of *Ficus tinctoria gibbosa,* which they eventually leave to the outside of the receptacle. Grandi (p. 114) stated as a peculiarity (for fig wasps!) that the male has not developed any "incarico per la liberazione della sua compagna" with which, of course, it mates outside the fig.

Eudecatominae

Of the fig wasps not belonging to either the Agaonidae or the Torymidae, this is the most important group. Many species were described from figs of the subgenus *Urostigma,* from Asia as well as from South America: these include several, originally classified with *Decatoma* (some differential characters of *Eudecatoma* and *Sycophila,* as most are now named, were given by Burks, 1971: 7). Boucek (1974: 268) noted that there seems to be little information about whether the sycophilous species are really confined to figs, as several others do develop in various galls on other plants, or are clearly associated with insects in grass stems. Joseph (1959b: 92) suggested a "cleptoparasitic" way of life for *Decatoma fici* in *Ficus virens;* Hill (1967c: 431) noted that *Sycophila* are probably phytophagous gall-formers, although they could be parasitizing the Epichrysomallinae. The structure of the female reproductive system was discussed by Copland & King (1972).

THE FIGS

In the lowland tropics of Asia and Australasia, the abundance of fig-species is a good measure of the richness of the environment in plant and animal life (Corner, 1967: 24, see also p. 32 ff.). *Ficus* is mainly defined by its syconium (i.e., in my opinion, by blastophagy), and this conceals the fact that *Ficus* has greater diversity in vegetative mechanism than any other genus of flowering plant and, indeed, of most families. From this basis, one expects a rather clear picture of the taxonomic subdivision of the genus, once the species are described and the synonymies revealed. Much as *Ficus* can be taken as an example of the phylogenetic history of its biota, the classification of its hymenopterous symbionts should conform. Indeed, most of the series and sections as defined by Corner (1965), prove to be paralleled by groups of wasps, especially those of the pollinating Agaonidae. The larger subdivision of *Ficus* in four taxonomic sections, however, is not in all parts reflected in the composition of the wasp fauna (table 8).

Table 8. The classifications of figs and wasps compared.

Ficus	Agaonidae	
	Agaoninae	Blastophaginae
UROSTIGMA		
Urostigma	*Elisabethiella* [1])	*Blastophaga*
Leucogyne		*Maniella*
Conosycea		*Blastophaga, Eupristina, Parapristina, Waterstoniella, Deilagaon*
Stilpnophyllum		*Blastophaga*
Malvanthera	*Pleistodontes*	*Blastophaga* [1])
Galoglychia	*Agaon, Alfonsiella, Allotriozoon, Elisabethiella, Nigeriella*	
Americana		*Pegoscapus*
PHARMACOSYCEA		
Pharmacosycea	*Tetrapus*	
Oreosycea		*Blastophaga, Dolichoris*
FICUS		
Ficus		*Blastophaga*
Rhizocladus		*Blastophaga*
Kalosyce		*Blastophaga*
Sinosycidium		*?*
Sycidium		*Liporrhopalum, Ceratosolen*
Adenosperma		*Ceratosolen*
Neomorphe		*Ceratosolen*
Sycocarpus		*Ceratosolen*
SYCOMORUS		*Ceratosolen*

[1] One species only; these records need confirmation. Several other, solitary, records of figs and wasps of uncertain classification are omitted.

A notable discrepancy, here discussed as one example of the joint effort of botany and entomology to arrive at an integrated classification, is found in the group pollinated by *Ceratosolen*-wasps viz., sections *Adenosperma, Neomorphe* and *Sycocarpus* of subgenus *Ficus*, and subgenus *Sycomorus*. Also with the messmates, three of these groups are exclusively characterized by the presence of one genus viz., *Apocrypta*, while one, *Sycomorus*, is characterized by the presence of *Sycophaga* (in Africa) and the absence of *Philotrypesis*. Some of the species classified with *Ceratosolen* (but none of *Apocrypta* and *Sycophaga*), are members of the entomofauna of other fig sections e.g., section *Sycidium* (*Ficus minahassae* with *Ceratosolen pygmaeus; F. pungens* with *C. nanus*); section *Ficus* (*F. pseudopalma* with *C. bakeri*); section *Oreosycea* (*F. pritchardii* with *C. marshalli*). Ramirez (1974), referring to his unpublished thesis, combined these species and groups, as well as *F. rivularis* ("probably pollinated by a *Ceratosolen* wasp"), all in a heap (subgenus *Sycomorus* in his sense). When I classified *Ceratosolen marshalli, nanus,* and *pygmaeus* (Wiebes, 1963a: 8–9, 85; two other species, from figs of section *Sycocarpus*, were tentatively placed in the same species-group), I did not know *Liporrhopalum*. Now, having at hand Hill's revision of *Liporrhopalum*, many of its characteristic features lead me to a revaluation of the three putative *Ceratosolen's*. Not all connections are clear yet, mainly because most groups of *Blastophaga* s.l. are still not revised, but I cannot now be as certain as I was twelve years ago, of any apparent affinity with *Ceratosolen*. As to the botanical place of *Ficus pritchardii*, a "problem is that, as a monoecious species [it] should belong in one of the subgenera *Urostigma, Pharmacosycea* or *Sycomorus*. It fits none and finds no aberrant alliance with any of their species" (Corner, 1970b: 401).

Ficus pseudopalma (as well as *F. rivularis*) differs from the rest of section *Ficus* markedly enough to require a separate taxonomic series (Corner, 1969b: 326); on p. 56 of 1967, Corner stated: "if *F. pseudopalma* had an entire perianth, which seems a detail, it would be close to *F. dammaropsis*" (section *Sycocarpus*). In the same paper of 1969 (b, fig. 5) Corner illustrated the intricate relationships between sections *Ficus* and *Sycocarpus*. In this diagram, *Auriculisperma* and *Sycocarpus* are derived from an ancestral *Ficus*, which also sends offshoots to section *Ficus* (with *Pseudopalmeae* as one of the early branches) and, separately, to *Rivulares*. It does not show *Sycomorus*, some species of which harbour wasps immediately related to those from *Neomorphe* (e.g., *F. oligodon* and *F. auriculata* with *Ceratosolen emarginatus*). *F. oligodon*, it should be noted, was formerly classified with *Sycocarpus* (subsection *Pomifera*) because of its saccate perianth covering the ovary: a prime respect in the classification of the genus (Corner, 1962: 395). In *Sycomorus*, the one Indo-Australian species (viz., *F. racemosa*) is peculiar in not having a symbiont of the genus *Sycophaga*, which is present in all African species; the figs are monoecious, while the *Ficus* sections mentioned above are dioecious.

In my opinion, as also published in 1973 (p. 24–25), the entomological evidence suggests a reclassification of the figs although this should wait, I hasten to add, until the evidence is more conclusive! The interplay of characters, as recorded in *Ficus*, may possibly be unravelled by the characters of the wasps. As our present knowledge of *Ceratosolen* indicates, the old classification of *Neomorphe* with *Sycomorus* appears to be confirmed, and its close alliance with *Sycocarpus* (*Covellia*) corroborated. This is not to suggest that the origin of *Sycocarpus* is to be sought in modern *Neomorphe* (Corner, 1962: 395, contradicted this), but they may form sister-groups which, of course, is what is meant by "alliance" or "taxonomic relationship". The monoecious condition found in *Sycomorus* as well as in a species of *Papuasycea*, may indicate the primitive state, whereas *Neomorphe* and *Sycocarpus* (etc.) may represent the derived dioecious condition. The pollinator of *Ficus pseudopalma*, in my opinion, gives away a close connection with primitive *Sycocarpus*, while the absence of *Apocrypta* from its entomofauna, may point to an early branching.

The completion of a laborious task is still before us: the inventory of the fig fauna, and the apprehension of the relations between figs and wasps. The combinations of characters then, once seen in a phylogenetic context, recognized as indicators of monophyletic groups of taxa and, eventually, understood in their biological meaning, may be used as arguments for a classification of their bearers: figs and wasps in symbiosis.

References

For convenience, this list includes only the references not given in Hill's (1967d: 107–124) bibliography, a few corrections (indicated by an asterisk), and additions to that bibliography. It is supposed to be complete up to and including most of the year 1975.

ABDURAHIMAN, U. C. & K. J. JOSEPH. 1967a. Contributions to our knowledge of fig insects (Chalcidoidea: parasitic Hymenoptera) from India (New Series) 1. Notes on some new and interesting fig-insects.— *Oriental Insects* **1**: 1–19.

———— 1967b. *Idem* 2. New fig insects from Delhi and correction of a mistaken identification.— *Bull. Ent. Loyola Coll.* **8**: 48-57.

———— 1975a. Three new Chalcidoidea (Hymenoptera) from India.— *Oriental Insects* **9**: 99–109.

———— 1975b. New fig insects (Hymenoptera : Chalcidoidea) from India: three Torymids parasitic on Agaonids.— *Entomophaga* **20**: 73–80.

ANSARI, M. H. 1967. The process of egg laying in Idarninae (Chalcidoidea: Hymenoptera). — *Ind. J. Ent.* **29**: 380–384.

BALTAZAR, C. R. 1966. A catalogue of Philippine Hymenoptera (with a bibliography, 1758–1963).— *Pacific Ins. Monogr.* **8**: 1–488.

BOUCEK, Z. 1974. On the Chalcidoidea (Hymenoptera) described by C. Rondani.— *Redia* **55**: 241–285.

BURKS, B. D. 1969. Redefinitions of two genera of Chalcidoids from figs, with new Florida species (Hymenoptera).— *Florida Ent.* **52**: 115-122.

———— 1971. A synopsis of the genera of the family Eurytomidae (Hymenoptera: Chalcidoidea).— *Trans. Am. ent. Soc.* **97**: 1–89.

CASTELLANOS, A. 1944. La especie de Ficus del noroeste Argentino.— *Lilloa* **10**: 483–491.

CHOPRA, R. N. & H. KAUR. 1969. Pollination and fertilization in some Ficus species.— *Beitr. Biol. Pflanzen* **45**: 441-446.

COPLAND, M. J. W. & P. E. KING. 1972. The structure of the female reproductive system in the Eurytomidae (Chalcidoidea: Hymenoptera).— *J. Zool.* (*London*) **166**: 185–212.

COPLAND, M. J. W., P. E. KING & D. S. HILL. 1973. The structure of the female reproductive system in the Agaonidae (Chalcidoidea, Hymenoptera).— *J. Ent.* (*London*) (*A*) **48**: 25–35.

CORNER, E. J. H. 1967. Ficus in the Solomon islands and its bearing on the post-Jurassic history of Melanesia.— *Phil. Trans. R. Soc. Lond.* (*B*) **253**: 23–159.

———— 1969a. The complex of Ficus deltoidea; a recent invasion of the Sunda Shelf.— *Ibid.* **256**: 281–317.

———— 1969b. Ficus sect. Adenosperma.—*Ibid.* **256**: 319–355.

———— 1970a. Ficus subgen. Ficus. Two rare and primitive pachycaul species.—*Ibid.* **259**: 353–381.

———— 1970b. Ficus subgen. Pharmacosycea with reference to the species of New Caledonia.— *Ibid.* **259**: 383–433.

———— 1975. Ficus in the New Hebrides.—*Ibid.* **272**: 343–367.

CROIZAT, L. 1968. The biogeography of the tropical lands and islands east of Suez-Madagascar: with particular reference to the dispersal and form-making of Ficus L., and different other vegetal and animal groups.— *Atti Ist. bot. Lab. Crittogam. Univ. Pavia* (*6*) **4**: 1–400.

———— 1969. A proposito di alcune critiche di E. J. H. Corner.— *Ibid.* **5**: 181–190.

EISEN, G. 1901. The fig: its history, culture and curing, with a descriptive catalogue of the known varieties of figs.—*Bull. Div. Pomol. U.S. Dept. Agric.* **9**: 1–317 [Bibliography: 295–301].

FORSKAL, P. 1775. Flora aegyptiaco-arabica: 1–32, i-cxxvi, 1–220.

GALIL, J. 1966. [The sycomore tree in the civilization of the Near East].— *Teva VeAretz* **8**: 306–318, 338–355 [Hebrew].

——————— 1967. Sycomore wasps from ancient Egyptian tombs.— *Israel J. Ent.* **2**: 1–10.

——————— 1968. An ancient technique for ripening sycomore fruit in East Mediterranean countries.— *Econ. Bot.* **22**: 178–190.

——————— 1973a. Topocentric and ethodynamic pollination.— *In* N. B. M. Brantjes (Ed.), Pollination and dispersal: 85–100.

——————— 1973b. Pollination in dioecious figs. Pollination of Ficus fistulosa by Ceratosolen hewitti.— *Gdns' Bull., Singapore* **26**: 303-311.

GALIL, J., R. DULBERGER & D. ROSEN. 1970. The effects of Sycophaga sycomori L. on the structure and development of the syconia in Ficus sycomorus L.— *New Phytol.* **69**: 103–111.

*GALIL, J. & D. EISIKOWITCH. 1965. [Pollination of the flowers of Ficus religiosa L.].— *Teva VeAretz* **7**: 1–16 [Hebrew].

——————— 1968a. On the pollination ecology of Ficus sycomorus in East Africa.— *Ecology* **49**: 259–269.

——————— 1968b. Flowering cycles and fruit types of Ficus sycomorus in Israel.— *New Phytol.* **67**: 745–758.

——————— 1968c. On the pollination ecology of Ficus religiosa in Israel.— *Phytomorphology* **18**: 356–363.

——————— 1969a. Further studies on the pollination ecology of Ficus sycomorus L. (Hymenoptera, Chalcidoidea, Agaonidae).— *Tijdschr. Ent.* **112**: 1–13.

——————— 1969b. Note on pollen transport, pollination and protection of ovaries in Ficus sycomorus.— *New Phytol.* **68**: 1243-1244.

——————— 1971. Studies on mutualistic symbiosis between synconia and sycophilous wasps in monoecious figs.— *Ibid.* **70**: 773–787.

——————— 1974. Further studies on pollination ecology in Ficus sycomorus ii. Pocket filling and emptying by Ceratosolen arabicus Mayr.— *Ibid.* **73**: 515–528.

GALIL, J., W. RAMIREZ B. & D. EISIKOWITCH. 1973. Pollination of Ficus costaricana and F. hemsleyana by Blastophaga estherae and B. tonduzi (Agaonidae) in Costa Rica.— *Tijdschr. Ent.* **116**: 175–183.

GALIL, J. & Y. SNITZER-PASTERNAK. 1970. Pollination in Ficus religiosa L. as connected with the structure and mode of action of the pollen pockets of Blastophaga quadraticeps Mayr.— *New Phytol.* **69**: 775–784.

——————— 1971. Note on pollination in Ficus religiosa L.— *Ent. Ber., Amst.* **31**: 123–124.

GALIL, J., M. ZERONI & D. BAR SHALOM. 1973 Carbon dioxide and ethylene effects in the co-ordination between the pollinator Blastophaga quadraticeps and the syconium in Ficus religiosa.— *New Phytol.* **72**: 1113–1127.

GALLESIO, G. 1820. Pomona italiana. Parte scientifica fasc. 1 contenente il trattato del fico: 81–103.

GAUD, S. M. & L. F. MARTORELL. 1973. New insect records for Puerto Rico.— *J. Agric. Univ. Puerto Rico* **57**: 247–254.

GIRAULT, A. A. 1917. Some new Australian chalcid-flies, mostly of the family Encyrtidae (Hymenoptera).—*Insecutor Inscit. menstr.* **5**: 29-37.

GORDH, G. 1975. The comparative external morphology and systematics of the neotropical parasitic fig wasp genus Idarnes (Hymenoptera: Torymidae.— *Univ. Kansas Sci. Bull.* **50**: 389-455.

GRANDI, G. 1967. La vita straordinaria degli insetti dei fichi.— *Scientia* **7** (102): 7.

*HASSELQUIST, F. 1757. Iter Palaestinum. Eller Resa til Heliga Landet forrattad ifran Ar 1749 til 1752, med Beskrifningar Ron, Anmarkingar ofver de markvardigste Naturalier: i-xiv, 1–619.

——————— 1762. Reise nach Pälästina in den Jahren von 1749 bis 1752. Auf Befehl Ihro Majestät der Königinn von Schweden herausgegeben von Carl Linnaeus: 1–17, 1–606.

*HEGARDT, C. 1749. Ficus.— *In* Caroli Linnaei Amoenitates Academicae 1 (2): 23–54.

HILL, D. S. 1967d. Figs (Ficus spp.) of Hong Kong: i-viii, 1–130 [Bibliography: 107–124].

——————— 1969. Revision of the genus Liporrhopalum Waterston, 1920 (Hymenoptera Chalcidoidea, Agaonidae.— *Zool. Verh.* **100**: 1–36.

——————— 1971. Wasps and figs.— *New Scient. & Science J.*: 144–146.

HOWARD, L. O. 1899. The present status of the caprifig experiments in California.— *Bull. Div. Ent. U.S. Dept. Agric.* (*n.s.*) **20**: 28–35.

*JOSEPH, K. J. 1957a. Contributions to our knowledge of fig insects (Chalcidoidea: parasitic Hymenoptera) from India vii. Descriptions of fifteen new and revision of some old species.— *Ann. Soc. ent. France* **125**: 97–133.

———— 1966. Taxonomy, biology and adaptations in fig insects (Chalcidoidea).— *Proc. 2nd All-India Congr. Zool.* **2**: 400–403.

———— 1967. Newer trends in the taxonomy of the fig-inhabiting Chalcidoidea.— *Bull. nat. Inst. Sci., India* **34**: 257–262.

JOSEPH, K. J. & U. C. ABDURAHIMAN. 1968. Descriptions of six new species of Decatoma (Chalcidoidea: Eurytomidae) from Ficus benghalensis L.— *Oriental Insects* **2**: 63-87.

———— 1969. Contributions to our knowledge of fig insects (Chalcidoidea: Hymenoptera) from India 4. Further descriptions of new fig insects from Ficus bengalensis L.— *Ibid.* **3**: 37–45.

LATREILLE, P. A. 1825. Familles naturelles du règne animal: i–vi, 1–570.

LEE, S. S. & C. H. TAN. 1973. Fig wasps (Hymenoptera, Chalcidoidea).— *Malay. Nat. J.* **26**: 112-119.

LICHTENSTEIN, J. L. 1919. Note préliminaire au sujet de Philotrypesis caricae Hass.— *Bull. Soc. ent. France*: 313-316.

NIKOLSKAJA, M. N. 1954. [Blastophaga-pollinator of the fig].— *Priroda, Leningrad* **5**: 107–108 [Russian].

PETERSEN, B. 1966. The Noona Dan Expedition, 1961–62. Insects and other land arthropods.— *Ent. Medd.* **34**: 283–304.

PRINCIPI, M. M. 1971. Guido Grandi e la sua opera.— *Boll. Ist. Ent. Univ. Bologna* **30**: 1–24.

RAMIREZ B., W. 1969. Fig wasps: mechanism of pollen transfer.— *Science* **163**: 580–581.

———— 1970a. Taxonomic and biological studies of neotropical fig wasps (Hymenoptera: Agaonidae).— *Univ. Kansas Sci. Bull.* **39**: 1–44.

———— 1970b. Host specificity of fig wasps (Agaonidae).— *Evolution* **24**: 680–691.

———— 1974. Coevolution of Ficus and Agaonidae.— *Ann. Missouri Bot. Gdn* **61**: 770–780.

ROBSON, T. B. 1911. Blastophaga in Australia.— *Rural Calif.* **35**: 307.

SANTIS, L. de. 1971. La fauna de Chalcidoideos de America del Sur.— *Bol. Soc. ent. Peru* **6**: 59–63.

*SAUNDERS, S. S. 1883a. Descriptions of three new genera and species of fig insects allied to Blastophaga from Calcutta, Australia, and Madagascar; with notes on their parasites and on the affinities of the respective races.— *Trans. ent. Soc. London*: 1–27.

———— 1883b. [Characterization of fig insects].— *Proc. ent. Soc. London*: v–vi.

*———— 1883c. On the Cynips caricae of Hasselquist and other fig-insects allied thereto; with descriptions of a new species from Australia.— *Trans. ent. Soc. London*: 383–392.

———— 1883d. [Exhibition of both sexes of Ichneumon ficarius . . .].— *Proc. ent. Soc. London*: xxxi–xxxii.

SAVAGE, C. G. 1924. Smyrna fig culture.— *J. S. Austra. Dept. Agric.* **28**: 401–421.

SISSON, R. F. 1970. The wasp that plays cupid to a fig.— *Nat. Geographic* **138**: 690–697.

TREUB, M. 1902. L'organe femelle et l'embryogénèse dans le Ficus hirta Vahl.— *Ann. Jard. bot., Buitenzorg* (*sér. 2*) **3**: 124–157.

VECHT, J. van der, 1973. Insekten zonder tal: een uitdaging.— *Versl. Ned. Akad. Wetensch. Amst.* (*Nat.*) **82**: 41–48.

WALKER, F. 1846. List of the Hymenopterous insects in the collection of the British Museum, part 1: 1–100.

WATERHOUSE, C. O. 1881. Remarks on the types of Cynips psenes and Cynips sycomori in the Linnean Collection.— *Proc. ent. Soc. London*: xli–xlii (and reply by Saunders: xlii–xlv).

WESTWOOD, J. O. 1883c. [Further descriptions of insects infesting figs; errata].— *Trans. ent. Soc. London*: vii.

WIEBES, J. T. 1967a. Indo-Malayan and Papuan fig wasps (Hymenoptera, Chalcidoidea) 5. Description of Otitesellini (Torymidae).— *Proc. Acad. Sci. Amst.* (*C*) **70**: 121–136.

———— 1967b. *Idem* 6. The genus Eujacobsonia Grandi (Torymidae).— *Zool. Meded., Leiden* **42**: 107–115.

———————— 1967c. Guadalia vissali nov. gen., nov. spec., a new fig wasp from the Solomon Islands (Hymenoptera, Torymidae, Otitesellini).— *Ent. Ber., Amst.* **27**: 214–218.

———————— 1967d. Polanisa Walker, 1875 (Insecta, Hymenoptera): proposed suppression under the plenary powers.— *Bull. zool. Nomencl.* **26**: 319–320; **31**: 24–26 (1974, Opinion no. 1018).

———————— 1967e. Redescription of Sycophaginae from Ceylon and India,with designation of lectotypes, and a world catalogue of the Otitesellini (Hymenoptera Chalcidoidea, Torymidae.— *Tijdschr. Ent.* **110**: 399–442.

———————— 1968a. Fig wasps from Israeli Ficus sycomorus and related East African species (Hymenoptera, Chalcidoidea) 2. Agaonidae (concluded) and Sycophagini.— *Zool. Meded., Leiden* **42**: 307–320.

———————— 1968b. Species of Agaon from Congo (Kinshasa), with notes on synonymy (Hymenoptera, Chalcidoidea).— *Proc. Acad. Sci. Amst.* (*C*) **71**: 346–355.

———————— 1968c. A new Pleistodontes (Hymenoptera Chalcidoidea, Agaonidae) from Rennell Island.— *Nat. Hist. Rennell Isl.* 5: 115–117.

———————— 1969a. Preliminary report on a collection of fig insects (Hymenoptera Chalcidoidea) from Ficus gnaphalocarpa.— *Mém. Inst. fond. Afr. noire* **84**: 401–402.

———————— 1969b. Philosycus, a new genus of fig wasps allied to Otitesella Westwood (Hymenoptera Chalcidoidea, Torymidae).— *Ann. Mus. R. Afr. centr., in 8, Zool.* **175**: 439–445.

———————— 1969c. Hymenoptera Agaonidae, with an introductory chapter on West African fig wasps.— *Ibid.* **175**: 449–464.

———————— 1970a. Revision of the Agaonidae described by J. Risbec, and notes on their Torymid symbionts (Hymenoptera, Chalcidoidea).— *Zool. Meded., Leiden* **45**: 1–16.

———————— 1970b. Vijgen en vijgewespen.— *In* K. H. Voous (Ed.), Biosystematiek: 180–206. 240–242.

———————— 1971. A new record of Allotriozoon prodigiosum Grandi, and description of its symbionts (Hymenoptera, Chalcidoidea).— *Mém. Inst. fond. Afr. noire* **86**: 367–383.

———————— 1972a. A new species of Agaon from Nigeria (Hymenoptera, Chalcidoidea).— *Ent. Ber., Amst.* **32**: 122-124.

———————— 1972b. The genus Alfonsiella Waterston (Hymenoptera, Chalcidoidea, Agaonidae).— *Zool. Meded., Leiden* **47**: 321-330.

———————— 1973. Phylogenetic specificity of figs and fig wasps.— *In* N.B.M. Branjes (Ed.), Pollination and dispersal: 21–25.

———————— 1974a. Nigeriella, a new genus of West African fig wasps allied to Elisabethiella Grandi (Hymenoptera Chalcidoidea, Agaonidae).— *Zool. Meded., Leiden* **48**: 29–42.

———————— 1974b. The fig wasp genus Diaziella Grandi (Hymenoptera Chalcidoidea, Torymidae Sycoecini).— *Proc. Acad. Sci. Amst.* (*C*) **77**: 295-300.

———————— 1974c. Species of Agaon Dalman and Allotriozoon Grandi from Africa and Malagasy (Hymenoptera Chalcidoidea, Agaonidae).— *Zool. Meded., Leiden* **48**: 123–143.

———————— 1974d. Philippine fig wasps 1. Records and descriptions of Otitesellini (Hymenoptera Chalcidoidea, Torymidae).— *Ibid.* **48**: 145–161.

———————— 1975. Fig insects from Aldabra (Hymenoptera, Chalcidoidea).— *Ibid.* **49**: 225–236.

———————— 1976. Indo-Malayan and Papuan fig wasps (Hymenoptera, Chalcidoidea) 7. Agaonidae, mainly caught at light.— In preparation.